

Variable chemical defence in the checkerspot butterfly *Euphydryas gillettii* (Lepidoptera: Nymphalidae)

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Abstract. 1. Like other checkerspots, *Euphydryas gillettii* butterflies may contain the defensive chemicals, iridoid glycosides, which are sequestered from their hostplants during larval feeding.

2. We analysed the iridoid glycoside content of *E. gillettii* adults from two different populations, Warm Lake, Idaho, and Granite Creek, Wyoming, that have different patterns of hostplant use.

3. Gas chromatographic analysis of thirty butterflies from the Wyoming population showed that they contained a mean of 1.27 (± 0.19 SE) % dry weight iridoid glycosides. Notably, 20% of these butterflies contained no detectable iridoid glycosides.

4. In contrast, nineteen butterflies from the Idaho population contained a mean of 3.89 (± 0.38 SE) % dry weight iridoid glycosides, and all butterflies contained iridoid glycosides.

5. These results illustrate how the chemical defence of herbivorous insects varies according to differential use of potential hostplants.

Key words. *Euphydryas gillettii*, checkerspot butterfly, iridoid glycosides, unpalatability, chemical defence, insect–plant interactions.

Introduction

Many insect species sequester chemicals from their larval or adult hostplants that serve to make the insects unpalatable to potential predators (Rothschild, 1972; Blum, 1981; Brower, 1984; Bowers, 1988). For such an insect, its degree of chemical defence is determined by variation in the amount of sequesterable chemicals available in the hostplant, which may be affected by plant species, individual, organ and ontogeny (McKey, 1979); coupled with sequestrative efficiency of the insect, potential metabolic alteration of the compounds, relative deterrence or toxicity of the compounds, concentration of compounds in the insect, and predator species involved (Fink & Brower, 1981; Bowers, 1988, 1992; Pasteels & Rowell-Rahier, 1991). For insects that feed on more than a single species of hostplant, variation in the amounts and kinds of chemicals found among these species may also influence the levels of chemical defences acquired by the insect herbivore (Brower, 1984; Belofsky *et al.*, 1989; Nelson, 1993a, b).

Therefore, for different populations of such insects, the de-

gree of chemical defence may vary substantially depending on the hostplant species available and the ability of the insects to sequester defensive compounds. Such variation may be important in the relative susceptibility of insects in different populations to predation, and may affect interpretation of results of studies of chemical defence in insects (e.g. Bowers *et al.*, 1992; Nelson, 1993a, b). Most studies do not examine chemical defence of different populations of putatively unpalatable insects, yet differences between populations may be substantial (e.g. Lynch & Martin, 1993).

Butterflies in the genus *Euphydryas* specialize on plants containing a particular group of plant secondary compounds, the iridoid glycosides (Bowers, 1983). Iridoids are monoterpenoid compounds found in about fifty families of plants (Bobbitt & Segebarth, 1969; Jensen, 1991). These compounds serve as larval feeding stimulants (Bowers, 1983) and may also influence adult oviposition choice (Bowers, 1991). Certain iridoid glycosides, notably the carbocyclic iridoids aucubin, catalpol, macfadienoside, antirrhinoside and methylshanziside, are sequestered by a variety of insects that feed on plants containing those compounds, notably butterflies of the genus *Euphydryas* (Bowers & Puttick, 1986; Gardner & Stermitz, 1988; L'Empereur & Stermitz, 1990a, b; Rimpler, 1991; Bowers, 1992). Other iridoid

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glycosides may be metabolized or excreted (Gardner & Stermitz, 1988). As a result, only certain hostplants contain iridoids that are sequesterable and so contribute to the unpalatability of the insects ingesting them.

Sequestration of iridoid glycosides may protect insects containing them from a variety of vertebrate (Bowers, 1980, 1981; Bowers & Farley, 1990) and invertebrate (Bowers, 1992; Stamp, 1992; De la Fuente *et al.*, 1994; Dyer & Bowers, 1994) predators. However, variation in iridoid glycoside concentrations among different insect populations has only rarely been examined (but see Bowers *et al.*, 1992; Rimpler, 1991).

Euphydryas gillettii is the rarest of the six species of *Euphydryas* in North America. Recorded populations (Williams, 1990) are concentrated in the mountainous regions of western Wyoming and Montana, central Idaho and southwestern Alberta. The primary hostplant of this species in most populations is twinberry, *Lonicera involucrata* (Rich.) Banks (Caprifoliaceae), as first reported by Comstock (1940). Although plants in the Caprifoliaceae contain iridoid glycosides, they are the secoiridoids (Bobbitt & Segebarth, 1969), a group of iridoids that do not appear to be sequesterable (Rimpler, 1991). However, early views of this butterfly being monophagous on *L. involucrata* (e.g. Comstock, 1940) have been superseded by more detailed observations indicating that *E. gillettii* adults can oviposit on several other plant species (Williams, 1990). Specifically, Williams (1990) notes that, in addition to *L. involucrata*, the following hostplant species are used for adult oviposition in some populations: *Lonicera caerulea* L. (Caprifoliaceae), *Valeriana occidentalis* Heller (Valerianaceae), *Pedicularis groenlandica* Retz. (Scrophulariaceae), *Veronica wormskjoldii* Roem & Schult. (Scrophulariaceae) (in litt, C. F. Gillette, 1985). Furthermore, we have observed post-diapause larvae feeding on *Castilleja linariaefolia* Benth. and on *Pedicularis bracteosa* Benth. (Scrophulariaceae).

To understand the importance of variation in larval hostplant use for adult chemical defence, we examined two populations of *E. gillettii* that have different patterns of adult oviposition and larval feeding: Granite Creek, Granite County, Wyoming, and Warm Lake, Valley County, Idaho. The sites of these populations were surveyed to identify the plant species that were used for adult oviposition and larval feeding. We then tested these hostplants for the presence of the two iridoid glycosides most commonly sequestered, aucubin and catalpol (Rimpler, 1991; Bowers, 1992). We also collected samples of adult butterflies from these two populations and analysed them for aucubin and catalpol.

Materials and Methods

Like other *Euphydryas* species, *E. gillettii* is univoltine, with a larval diapause in the second, third or fourth instar (Williams *et al.*, 1984). In some populations individuals may diapause over two successive winters, emerging to feed for a short period in the intervening summer and returning to diapause; then continuing to feed, pupating, and eclosing the following summer (Williams *et al.*, 1984). Adults usually fly during July and sometimes into August. Females lay large numbers of eggs in masses, and larvae are generally gregarious in the earlier instars, but aggregations break up and larvae may wander substantial distances

to find food in the last two instars (Williams *et al.*, 1984). As a result, larvae often leave the hostplant at the time that they ingest the most food and have the potential to sequester the largest portion of their defensive compounds.

The two populations we studied differed substantially in a variety of features. The Granite Creek population was located at 2130 m (7000 ft) elevation, in the Gros Ventre Mountains of western Wyoming. Here we could find oviposition on only *L. involucrata*, but post-diapause larvae were observed feeding on two species of *Castilleja*, as well as on *L. involucrata*. The Warm Lake population, at 1630 m (5350 ft) elevation in the Boise National Forest, Idaho, is quite different. Females commonly oviposit on three different hostplant species, *L. involucrata*, *L. caerulea* and *Pedicularis groenlandica*. Feeding tests showed that pre-diapause larvae from this population performed equally well on all three of these hostplants (Williams, 1990). In addition to these three hostplant species, post-diapause larvae in this population also feed on *Castilleja* spp.

All butterflies were collected as adults in the field. They were kept alive and cool until they could be frozen at -70°C for subsequent chemical analysis. For analysis, they were dried at 50°C and ground to a fine powder before extraction and preparation for gas chromatography. Several specimens (three to six) of each of the plant species used by larvae or adults were also collected at the two sites. These were also dried at 50°C and ground to a homogenous powder, with 100 mg subsamples of the powder taken for analysis.

The concentrations of aucubin and catalpol were determined by gas chromatography for both insects and plants (Gardner & Stermitz, 1988; Fajer *et al.*, 1992; Bowers & Collinge, 1992; Bowers & Stamp, 1992). Each sample was prepared by extracting overnight in methanol. The solution was then filtered and the extract evaporated to dryness and partitioned between water and ether. The ether fraction, containing lipophilic substances, was discarded, and the water fraction containing primarily the iridoid glycosides and sugars was evaporated to dryness. An aliquot of this remainder was derivatized using Tri-Sil Z^T (Pierce Chemical Company), prior to injection into the gas chromatograph.

Two-way analysis of variance (ANOVA) was used to compare the iridoid glycoside concentration (as per cent dry weight) of males and females from the two populations. All concentrations were arcsine-transformed for analysis.

Results

Gas chromatography of the plants showed that *Pedicularis groenlandica* (Scrophulariaceae) contained only aucubin (0.51% dry weight) and *Castilleja linariaefolia* (Scrophulariaceae) contained both aucubin (0.73%) and catalpol (2.22%). No aucubin or catalpol was found in *Lonicera involucrata*, *L. caerulea* (Caprifoliaceae) or *V. occidentalis* (Valerianaceae).

Butterflies from the two populations were quite different in their overall iridoid glycoside concentrations (Fig. 1, Table 1). ANOVA showed that males and females from the same population did not differ in their iridoid glycoside content; however, the butterflies from the Idaho population had concentrations of iridoid glycosides about 3 times higher than those from the Wyoming population (Fig. 1, Table 1).

tected themselves, they may be protected by their automimetic resemblance (Brower *et al.*, 1968, 1970) to individuals that have acquired iridoid glycosides from some of the secondary hostplants that do contain sequesterable iridoid glycosides, such as *Castilleja* or *Pedicularis* species.

Decisions by *E. gillettii* females about where to oviposit may be affected more by environmental constraints due to the short growing season (Williams & Bowers, 1987) than by the potential for chemical protection of their offspring. Williams (1981) showed that the amount of time available for egg development is very short in habitats such as those of our study populations. Therefore eggs that do not have the appropriate orientation to the sun may not hatch before the leaves of the hostplant senesce at the end of summer (Williams, 1981). Because larvae may leave the maternally chosen hostplant in later instars and acquire sequesterable iridoids from other hostplant species, choice of an oviposition site in an appropriate microhabitat may be more important than the potential for chemical protection of the early-instar larvae.

The variation that we found among individual butterflies within each of the populations suggests that the hostplants used by the larvae were quite variable in their iridoid glycoside content, that larvae vary substantially in their ability to sequester iridoid glycosides, or that larvae may switch between plant species with and without sequesterable iridoid glycosides. In addition, the patterns of chemical variation observed in butterflies from the two populations were different, and the chemical data from the Wyoming population showed that 20% of the butterflies never fed on plants containing sequesterable iridoid glycosides. Since our observations indicate that females oviposit primarily or exclusively on *L. involucrata* in this population, larvae that do not leave this plant do not acquire sequesterable iridoid glycosides. In contrast, individuals that switch to other aucubin- or catalpol-containing hostplants may be able to acquire relatively large amounts of those compounds. These relatively unpalatable individuals can provide the models that protect palatable individuals, due to automimicry.

A previous series of feeding experiments using grey jays, *Perisoreus canadensis* (Corvidae), showed that *E. gillettii*, from the same Wyoming population from which we obtained butterflies used in this study, were relatively palatable, whereas two other *Euphydryas* species, *E. phaeton* from Massachusetts and *E. anicia* from Colorado, were relatively unpalatable (Bowers & Farley, 1990). The chemical data provided in the present paper suggest that one reason for the observed palatability of *E. gillettii* in the earlier feeding experiments is the relatively low (or zero) concentrations of iridoid glycosides found in butterflies from this Wyoming population.

Although automimicry may be important in *E. gillettii*, there may also be mimicry of other checkerspot butterflies that have higher or more predictable levels of unpalatability. Both *Euphydryas anicia* and *E. editha* may fly in the same habitats as *E. gillettii* and are visually very similar (see Howe, 1975). Both these species contain iridoid glycosides (Gardner & Stermitz, 1988; Bowers, 1992) and do not generally use plant species that have only secoiridoids as hostplants (Bowers, 1983); they are therefore quite well protected with relatively high levels of iridoid glycosides (up to 9% dry weight; Gardner & Stermitz, 1988).

The mimetic resemblance among these three species (or between pairs of these species) may therefore be a rather complex combination of automimicry, coupled with a continuum from Batesian to Mullerian mimicry.

Data from monarch and queen butterflies (*Danaus plexippus* L. and *D. gillippus*) provide a valuable comparison with these data from *E. gillettii* and data from other species of *Euphydryas* (Bowers & Puttick, 1986; Gardner Stermitz, 1988; Belofsky *et al.*, 1989; Bowers, 1991). For example, monarchs and queens also exhibit substantial variation in cardenolide concentrations (Roeske *et al.*, 1976; Fink & Brower, 1981; Cohen, 1985). In these two *Danaus* species, as in *Euphydryas*, concentration of defensive chemicals in the insects is related to hostplant chemistry and its variation (e.g. Roeske *et al.*, 1976; Cohen, 1985; Lynch & Martin, 1993; Nelson, 1993a), sequestrative efficiency of the insects (Nelson, 1993b; Cohen, 1985) and whether particular compounds are sequestered, metabolized or eliminated (Roeske *et al.*, 1976). In both *Danaus* and *Euphydryas*, hostplant chemistry and its variation may be the critical determinant of insect palatability and defence against potential predators.

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Table 1. Results of two-way ANOVAs on arcsine-transformed values of iridoid glycoside concentrations of male and female *Euphydryas gillettii* from two populations, Idaho and Wyoming.

Factor	Aucubin concentration		Catalpol concentration		Total iridoid glycosides	
	F	P	F	P	F	P
Population	16.363	<0.001	6.499	<0.02	19.120	<0.001
Sex	0.094	n.s.	0.189	n.s.	0.150	n.s.
Population × Sex	0.265	n.s.	0.241	n.s.	0.279	n.s.

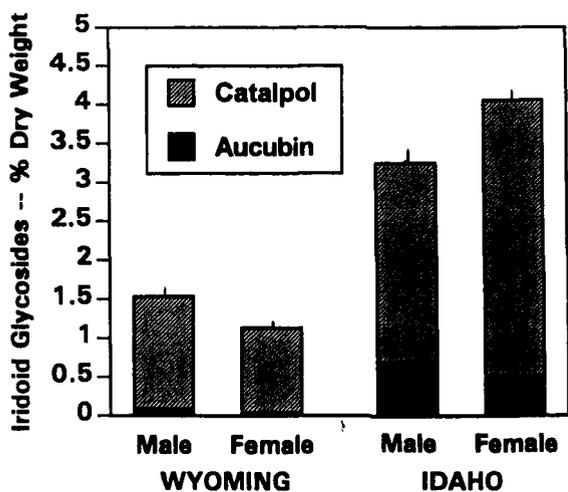


Fig. 1. Concentrations of aucubin and catalpol (% dry weight) of male and female *Euphydryas gillettii* from populations in Wyoming and Idaho. Means ± standard errors are shown.

In addition, butterflies from both populations were quite variable in the amounts of iridoid glycosides they contained (Fig. 2): the range of total iridoid glycoside concentrations was 0–3.99% dry weight ($n = 30$) from the Wyoming population and 0.29–6.00% dry weight ($n = 19$) from the Idaho population. Notably, 20% ($n = 6$) of the butterflies from the Wyoming population contained no aucubin or catalpol, whereas all the butterflies from the Idaho population contained one or both of these compounds. For butterflies from both populations, most of the iridoid glycoside we detected was catalpol. The proportion of total iridoid glycosides that was catalpol in individual butterflies ranged from 0.61 to 1.00 in the Wyoming population and from 0.28 to 1.00 in the Idaho population.

Discussion

Because *L.involucrata*, *L.caerulea* and *V.occidentalis* do not contain any sequesterable iridoids, larvae from eggs oviposited on those plants can only sequester iridoid glycosides if they leave the initial hostplant. However, if the larvae do not switch to alternative hostplants and are consequently not chemically pro-

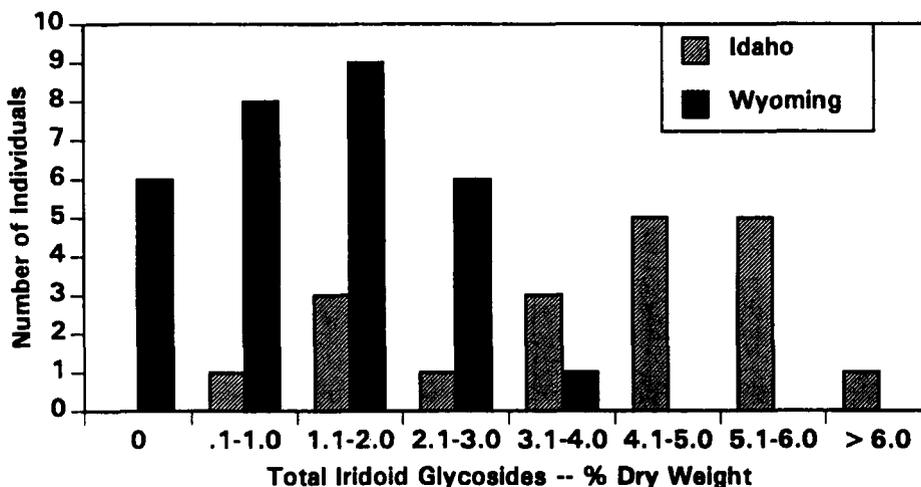


Fig. 2. Distribution of total iridoid glycoside concentrations among individual *E.gillettii* butterflies from Wyoming and Idaho. Data from aucubin and catalpol are combined to indicate total iridoid glycoside concentrations (% dry weight), and data from males and females are not separated.